Great Basin Naturalist 53(2), pp. 145-16H

LATE QUATERNARY VEGETATION AND CLIMATE IN THE ESCALANTE RIVER BASIN ON THE CENTRAL COLORADO PLATEAU

Kim Withers¹ and Jim 1. $Mead^2$

ABSTRACT.—Five alcoves (rock shelters) in the Forty-Mile Canyon–Willow Gulch area of the Escalante River Basin in southeastern Utah yielded rich deposits of late Quaternary macrobotanical remains. The deposits were sampled and the contents identified in order to construct a chronology of vegetational change. Fourteen radiocarbon dates indicate that the fossils were deposited between 12,690 and 7510 vr B.P. (vears before present).

Ninety-one plant taxa were identified, 62 to species. Six species were common to all alcoves: Gambel oak (*Quercus gambelii*), box-elder (*Acer negundo*), prickly pear (*Opuntia* subgenus Platyopuntia), skunkbush (*Rhus aromatica var. trilobata*), serviceberry (*Anclanchier utahensis*), and Indian ricegrass (*Oryzopsis hypernoides*).

Late Pleistocene samples (>11,000 yr B.P.) contain extralocal, elevationally depressed species such as Douglas fir (*Pseudotsuga menziesii*), spruce (*Picea* sp.), and mountain mahogany (*Cercocarpus ledifolius*), and mesophytic species such as rose (*Rosa woodsii*) and water birch (*Betula occidentalis*). Early Holocene samples (11,000–5000 yr B.P.) contain no elevationally depressed conifers, and the remaining mesophytic species decrease in relative abundance. Reticulated hackberry (*Celtis reticulata*) becomes common. The terminal Early Holocene sample (5000–7000 yr B.P.) contains abundant Gambel oak and prickly pear, but little else.

Paleoclimatic interpretations for the Late Pleistocene correspond well to those of most other workers on the Colorado Plateau. Climates that were wetter and at least seasonally cooler than they are today are inferred from the macrobotanical assemblage. However, the increased moisture is attributed to higher stream base levels and increased groundwater rather than directly to increased precipitation. Early Holocene climates are interpreted as warmer and drier than those of the Late Pleistocene but still wetter than the present climate. Groundwater levels appear to be decreasing due to stream entrenchment. Terminal Early Holocene climates were much warmer and at least seasonally drier. By the end of the period, groundwater levels had decreased so much that the alcoves were unable to sustain plant communities; stream base level was probably near the present level.

Key words: Quaternary, Colorado Plateau, plants, oak, Quercus, Pleistocene.

The Colorado Plateau has been the focus of late Quaternary paleoecologic work in the last decade; however, the late Quaternary plant communities of the central plateau, southeastern Utah, are still inadequately known because of the few case studies conducted. Late Pleistocene-Early Holocene plant communities of the central plateau have been described using macrofossils found in the alluvial deposits from Cowboy Cave (Spaulding and Peterson 1980, Spaulding and Van Devender 1980), from scattered packrat (Neotoma spp.) middens from the Paradox Basin (Betancourt 1984, 1990), and from the megaherbivore dung blankets from Bechan Cave (Davis et al. 1984, Mead et al. 1986), Cowboy Cave (Hansen 1980), and various alcoves (Mead and Agenbroad 1989, 1992).

The macrofossils in this study (Withers 1989) were excavated from sandstone alcove (rock shelter) allowium and thus can represent only the community of the microhabitat where the deposit was found. The objectives of this research were to describe and to explore the paleoenvironmental implications of changes in plant communities through time.

STUDY AREA

From 1986 to 1988 field crews from Quaternary Studies Program, Northern Arizona University, explored several alcoves in the Forty-Mile Canyon and Willow Gulch areas of the Escalante River Basin (Glen Canyon National Recreation Area: Fig. 1), which is the eastern boundary of the Kaiparowits Basin. Because

Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77543.

²Quaternary Studies Program and Department of Geology, Northern Arizona University, Boy 5644, Flagstaff, Arizona S6011. Address for all correspondence

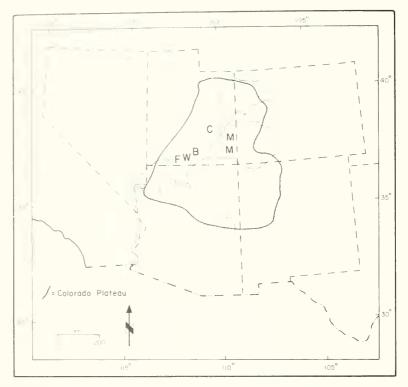


Fig. 1: Map of the Southwest locating the Colorado Plateau (delineated by stipples). F, Forty-Mile Canyon; W, Willow Gufch. B. Bechan Cave; C. Cowboy Cave; M. midden studies of Betancourt (1984, 1990).

our study is on lands administered by the National Park Service, we were requested not to locate the alcoves (on a map or in a description) with any precision. Somewhat more detailed descriptions of the alcoves are in Mead and Agenbroad 1992. Anyone needing further descriptions of locations may contact the regional scientist at the Rocky Mountain Regional Office. Denver Colorado, At least S51 plant taxa presently live in the Kaiparowits Basin, resulting in many diverse local plant associations (Welsh et al. 1975). Taxonomic terminology follows Welsh et al. 1987.

The canyons cut through the Navajo Sandstone and the upper units of the more resistant Kayenta Formation. The alcoves appear to have been formed in the cross-bedded sandstone by spalling wall extohation – facilitated by the action of morsture infiltration, through joint-controlled surface drainage. All alcoves in this dramage area appear unique because they conum perched terraces, which are remnants of another thevial deposits. It is estimated that the area of he fluxial deposits exceeds 30,000 years (Agenbroad and Mead manuscript). Stratified fluvial sediments are usually found on either side of steep talus slopes that are composed of sandstone blocks and boulders overlain by eolian sand. These talus slopes often contain prominent layers of macrobotanical fossils and other remains such as bones, hair, and dung. Five alcoves were chosen for study based on the abundance of plant remains evident in the deposits.

MODERN ENVIRONMENTS

Climate of the Escalante Basin is warm and semiarid with highly variable amounts of annual precipitation. Strong orographic gradients are exhibited by both temperature and precipitation. Mean annual temperature of low-elevation sites along the river is 12°C, with 250 mm or less mean annual precipitation. At high-elevation sites in the nearby Aquarius Plateau, mean annual temperature is 2°C, with 575 mm of mean annual precipitation (Webb 1985). Vegetation in the basin ranges from Great Basin desertscrub to spruce-fir (*Picea* spp.– *Abies* spp.) forest. Low areas between 1400 m and 1700 m elevation are a mixture of shrublands and grassland (Tanner 1940). Pinyon-juniper (*Pinus* spp.–*Juniperus* spp.) woodland occurs between 1800 m and 2300 m, followed by a yellow pine-oak-manzanita (*Pinus ponderosa–Quercus* spp.–*Arctostaphylos pungens*) association between 2300 m and 2700 m. Above 2700 m, the southern face and top of the Aquarius Plateau support a spruce-fir forest (Webb 1985).

Topography in the immediate area of Forty-Mile Canyon and Willow Gulch is diverse. Elevation ranges from 2300 m at the top of the Kaiparowits Plateau, where the perennial streams that carve the canyons begin, to about 1100 m at the confluence of the two canyons at the Escalante River.

Pinvon-juniper woodland dominates between 2300 m and 1500 m. Below the woodland on benches and in slick-rock areas is desertsernb dominated by blackbrush (Coleogyne ramosissima). Within the canyons, habitats range from nearly vertical rock faces to valleylike areas; from dry, rocky slopes and creekbeds with active, steep sand dunes to riparian woodlands and hanging gardens. Valley areas are dissected by sandy washes. Many plant species such as skunkbush (Rhus aromatica var. trilobata), single-leaf ash (Fraxinns anomala), barberry (Mahonia fremontii), and serviceberry (Amelanchier utahensis) are found throughout the creek system in a variety of habitats, while others such as willow (Salix spp.), tamarisk (Tamarix ramosissima, introduced), box-elder (Acer negundo), and seep willow (Baccaris emoryi) are found only near permanent running water. Cottonwood (Populus fremontii) is common along permanent watercourses as well as areas where groundwater is near the surface.

On dry slopes above the streambed, important species include skunkbush, sagebrush (Artemisia spp.), blackbrush, snakeweed (*Cuticrrezia* spp.), prickly pear, brickellbush (Brickellia californica, B. grandiflora), and Indian ricegrass (*Oryzopsis hymenoides*). In valleys many of these same species are common along with winter fat (*Ceratoides lanata*) and scattered individuals of Utah juniper, single-leaf ash, netleaf hackberry (*Celtis reticulata*), and cliff-rose (*Purshia mexicana*). Hackberry is widespread but uncommon, usually occurring in sheltered, shady areas.

Gambel oak (*Quercus gambelii*) is common in wet, shady areas and hanging gardens in Willow Gulch but is restricted to a relictual population in a valleylike area in the upper part of Forty-Mile Canyon. There it is found only on the shady, north-facing side of the canyon against the rocks and on the sides and bottoms of deep, sandy washes. Shrub live oak (*Q. turbinella*) is common in the upper reaches of both canyons but becomes rare as the alluvium becomes wetter. Shinnery oak (*Q. havardii*) is restricted to the driest, uppermost portions of the canyons.

In the wettest parts of the canyons, near seeps and at the edge of the creek, important species include horsetail (*Equisetum* spp.), common reed (*Phragmites australis*), sedges (*Carex* spp., *Scirpus* spp.), birchleaf buckthorn (*Rhamnus betnlaefolia*), and saltgrass (*Distichlis spicata*). Box-elder is found scattered along the canyon bottom and occasionally in hanging gardens. Common hanging garden species include varions ferns and mosses as well as poison ivy (*Toxicodendron rydbergii*), cardinal flower (*Lobelia cardinalis*), watercress (*Nasturtium officinale*), cardinal monkeyflower (*Minulus cardinalis*), and columbine (*Aquilegia micrantha*).

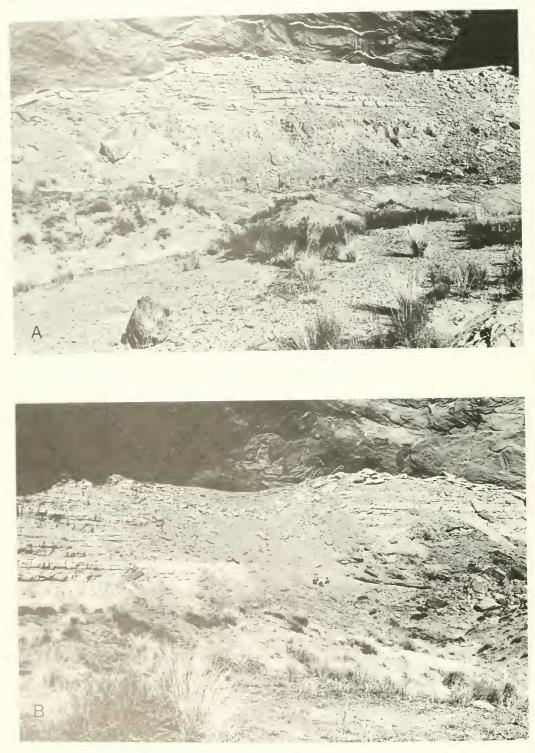
FOSSIL LOCALITIES

Hooper's Hollow, Grobot Grotto, and BF Alcove are in Forty-Mile Canyon; Shrub-Ox Alcove and Oak Haven are in Willow Gulch (Fig. 1). All are located between 1100 and 1300 m in elevation.

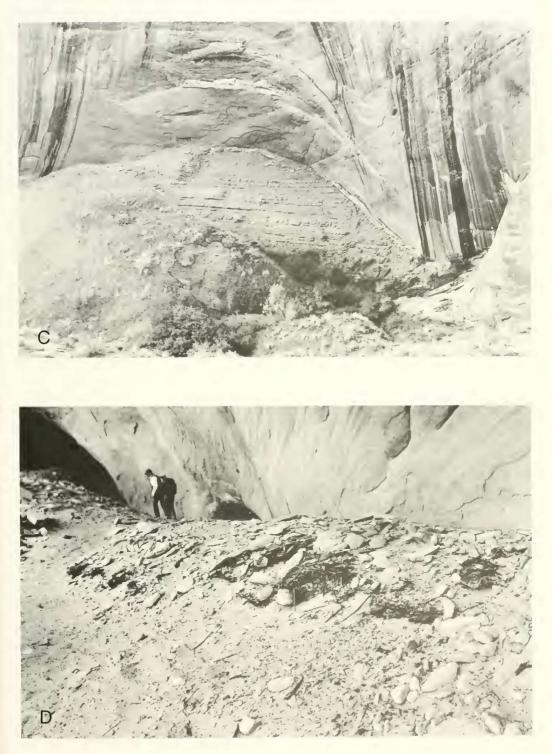
Forty-Mile Canyon

The alcoves in Forty-Mile Canyon are difficult to reach. Approximately 10 m of vertical or nearly vertical sandstone rises from the deeply entrenched streambed to the base of the alcoves. Streamside vegetation below BF Alcove and Grobot Grotto is dominated by willow and tamarisk, but there is little streamside vegetation below Hooper's Hollow.

Hooper's Hollow and Grobot Grotto are large (100–200 m wide), sonthwest-facing alcoves (Fig. 2). Tops of the deposits in both are at approximately 1200 m elevation. In both alcoves modern vegetation is characterized by desert grassland species, with a few scattered shrubs. Active and grass-stabilized sand dunes,



Examples of alcoves mentioned in text: A, Hooper's Hollow; B, Grobot Grotto; C, Bl people for scale in center of B; units containing macrobotanical remains occur about the roc deposit. Drv-preserved botanical remains occur stratigraphically above the layered, fluvial arc and the basic units at all alcoves; sediments are of Sangamonian age.



it well is large reaced shell-rock sandstone, are uso found. Indian (ricegrass is the dominant pecies. Other species noted in the area include indigobush *Psorothannus fremontii*). Mormon tea, *Ephedra viridis*, snakeweed, porempine prickly pear *Opuntia crinacea*), buckwheat *Errogonum inflatum*, and dogweed *Dyssodia* pentachaeta).

BF Alcove is relatively narrow and faces northeast Fig. 2. It is the highest alcove in this study at about 1250 m elevation. The area just outside the alcove is a steep, grass-covered sand dune. Species present include Indian ricegrass, dropseed (*Sporobolus* sp.), and occasionally Mormon tea and snakeweed.

Willow Guleh

The alcoves in Willow Gulch are presently fairly easy to enter, usually requiring only a short climb up a steep embankment or sand dune. Shrub-Ox Alcove is located in a wide, valleylike area at 1190 m elevation and faces northwest. Cambel oak and shrub live oak grow near the stream below the alcove. Skimkbush, barberry, and brickellbush are common. Cottonwood is abundant near the creekbed and Indian ricegrass is widespread. Juniper trees are scattered across the valley. Porcupine prickly pear and hedge log cactus (*Echinocereus* sp.) are found growing in cracks in the sandstone.

Oak Haven is the lowest alcove in this study at 1140 m elevation and faces nearly due west (Fig. 2). It is narrow and shelflike, with a fairly large, rubble-filled shelter on the north end. It is a wet, "active" alcove, although not so wet as to destroy the fossils, about 50 m above the present streambed.

This is the only alcove in which species found in fossil samples still occur alive today. Gambel oak is abundant throughont the alcove. Other irboreal species found in or near the alcove are hackberry and box-elder. Common shribs inbide seep willow sacred datura (*Datura metel alex*) serviceberry, skinikbush, roundleaf hult hoberry. *Shepherdia rotundifolia*), and are brush. A plunge pool is located to the south the alcove and contains common hanging an lear pecies.

The tore contain two major sedimentary fluvial layers without organic reasons and the fluvial layers with fossils. I fluvial sediments, of which the auting filled the alcoves and the fluvial sediment into prior to 30,000 yr B.P. They were deposited when the canyou stream was dammed downstream, possibly by either a sand dune or canyon wall collapse. At any point during deposition behind the dam, the canyon would have contained fluvial (and possibly colian) units in the stream channel area, but there would have been lateral facies of colluvial deposition in the alcoves. Once the sediment depth had reached the threshold of the dam height, fluvial deposition would have ceased: however, lateral colluvial deposition would have continued. We are recovering fossils in the lateral colluvial facies.

When the dam was breached, sediments were probably downcut rapidly in at least the main streambed. Remaining sediments were eroded from behind and beneath by groundwater flowing between the sediments and sandstone (seeps and springs). They were also eroded by channeling and water flowing over the surface, especially at the alcove dripline. Remnants were left behind as predominantly the lateral facies in the alcoves. The oldest dated laver from our study, ca. 23,000 vr B.P. (SOA4), as well as manimoth (Manimutluis) dung from below the profile in Grobot Grotto, which dates ca. 26,000 vr B.P. (Mead and Agenbroad 1989), is evidence that the valley sediments had already been extensively eroded by the last full glacial (ca. 21,000 yr B.P.).

Depositional Environments and Taphonomy

The taphonomy (what happens to organic remains after death) of the localities is important to understand. Organic remains are preserved in the alcoves behind the dripline, that is, inside the shelter and away from direct effects of precipitation. Fossil remains were incorporated into the alcove sediment layers conceivably by various methods.

(1) A plant taxon could have washed into the alcove, meaning that the plant actually grew at a different location (possibly at a much higher elevation and in a different community) and was carried by stream action to a lower elevation, to finally come to deposition in one of our alcoves. Had this been the scenario, the matrix immediately around the plant remains would be fluvial in nature. The sediments would show some sort of stream action or deposition. Even the plant remains would show some sort of transport damage—which they do not show. This is not the case. (2) A plant taxon could have been carried into the alcove by wind action. For this scenario to realistically happen, the taxon in question would have had to grow nearby enough to be carried into the alcove by wind. Long-distance transport of so many fossils is not likely given the present physiographic situation. Certainly the taxon could have lived on the land above the alcove—which is now mostly narrow slick-rock. Having any of the fossil plants recovered in the alcove actually growing above the alcove, imstead of in the canyon, does not really alter our overall conclusions.

And finally, (3) a plant taxon could have been growing in or immediately outside the alcove. Plants in this scenario would have pristine macrofragments, except for situations where spalling wall rock damaged the specimens. The encasing sediments imply that only a colluvial (spalling) depositional environment is present.

It is our opinion that given the three possible depositional scenarios outlined above, the alcove and the fossils discussed here are the result of, at least predominantly, in situ deposition; that is, species actually grew inside or in the immediate vicinity of the alcove.

METHODS

Macrobotanical Fossil Collection and Analysis

Macrofossils were found in unconsolidated layers (leafmats) in the deposits or mixed with spall sands and blocks. Samples were difficult to obtain because the truncated deposits were very steep and loose (at angle of repose). Exposed surfaces were cleaned to remove loose, contaminating slumpage. The in situ leafmats were sampled by removing the mass of leaves, twigs, and other plant materials by hand or with a trowel. In between the leafmats or where plant remains were found mixed with the sand, bulk samples of sediment were collected.

Samples were taken from various locations within each site so that an accurate description of the plant community and a chronology of the site could be constructed. Generally, layers were sampled along a vertical line (profile) from the top of the deposit. At Oak Haven, Grobot Grotto, and Shrub-Ox Alcove, samples were also taken to the side of the main profile to test as much of the variability of each layer as possible. At BF Alcove, a 0.25-m pit was excavated and bulk-sampled at 10-cm intervals. These samples were dry-screened through 1-mm mesh at the site. Because the sand was so loose, it was nearly impossible to avoid mixing the layers along the edges of the pit. When sterile sand was found at 40 cm, the excavation was terminated and the pit backfilled. A similar pit was excavated at the top of the deposit (Holocene) at Grobot Grotto; however, the same slumpage problems were encountered. Since recovery was minimal, excavation was terminated at 30 cm.

In the Laboratory of Quaternary Paleontology (Northern Arizona University), bulk samples were dry-screened through a 20-mesh (0.84-mm) soil screen. They were identified by using the modern collection housed in the Museum of Northern Arizona Herbarium, consulting with various members of the biology faculty at Northern Arizona University, and examining regional literature (Gould 1951, Martin and Barkley 1961, Morris et al. 1962, Delorit 1970, Elmore 1976, Albee 1979, Welsh 1986, Welsh et al. 1987; Table 2). Plants were identified from twigs, leaves, seeds, flowers, flower parts (especially involucres), and fruits. Since the original mass and the number of unidentifiable fragments varied from sample to sample, all identified parts were counted and assigned a relative abundance according to the following scale: 1 =rare (1-2 fragments), 2 = uncommon (3-10)fragments), 3 = common (11-50 fragments), 4= very common (51–100 fragments), 5 = abundant (>100 fragments) (following Van Devender 1973).

Radiocarbon Dating

When possible, radiocarbon dates were obtained on a single species from a single layer. In cases where no single species was abundant, a composite sample of a single species from two layers (BF Alcove) or a plant species and some fecal material from a single layer (Oak Haven) were used. Multiple dating procedures were performed in each alcove to establish a chronology. All radiocarbon dating was done by Beta Analytic Incorporated. Coral Gables, Florida (Table 1).

RESULTS

Ninety-one fossil taxa were identified, 62 to species (Withers 1989). Of those, only six were common to all alcoves: Gambel oak, box-elder, serviceberry, prickly pear, skunkbush, and Indian ricegrass. Fourteen radiocarbon dates were

uql	Rad ocarbon date Ar B P	Lab no.	Material dated				
		Grobot Grotto					
.(,()	none		_				
.(.)	none						
.(.2	7510 - 160	20999	<i>Quercus gambelii</i> branch				
(.5	9730 + 170	20995	<i>Quercus gambelii</i> branch				
6.1	none		_				
65	99 <u>2</u> 0 → 100	20999	<i>Quercus gambelii</i> trunk				
		BF Alcove					
F	11,790 = 190	14727	Dung				
	12,130 - 170	20995	Pseudotsuga menziesii needles				
		Hooper's Hollow					
	10.630 - 110	25412	<i>Quercus gambelii</i> twigs				
112	$12,010 \pm 110$	25411	Quercus gambelii twigs				
		Shrub-Ox Alcove					
) \]	\$520 + \$0	25415	Quercus gambelii twigs				
) \ 2	5530 + 190	25656	<i>Quercus gambelii</i> twigs				
) \.3	$12,690 \pm 180$	25416	Quercus gambelii twigs				
)/1	$23,100 \pm 660$	25413	<i>Quercus</i> sp. limb fragment				
		Oak Haven					
ET 1	9150 + 100	28929	<i>Quercus gambelii</i> branch				
112	11,690 + 120	25418	<i>Rosa woodsii</i> twigs				
113	$^{\circ}9470 \pm 150$	25657	<i>Picea</i> sp. twigs and dung				
EE E	none	-	-				

Kalbergerer Betalab , in stratigraphic order, for Forty-Mile Canyon and Willow Gulch samples. I C. 1. C. Gutto, S.F. BE Alcove, HH, Hooper's Hollow; SOA, Shrub-Ox Alcove; OH, Óak Haven.

Dation of a Sectext

obtained to determine the age of the deposits. Materials dated included Gambel oak wood, rose *Rosa woodsii*) branches, Donglas fir needles, spruce twigs, and dung (Table 1).

Forty-Mile Canvon

GROBOT GROTTO – Excavation into Holocone sediments at the top of the deposit yielded few macrofossils: and since there was no obvious stratigraphy they were treated as one sample, GG0 not dated. This sample is identical to the modern flora as observed elsewhere in the canyon.

Four samples were collected from the 275cm-thick Gambel oak leaf-roof spall layer that began 157 cm downslope from the datum at the top of the deposit. Two of these samples containing Gambel oak were submitted for radiocarbon dating. Twigs from the top a dinear the bottom of the oak leaf layer dated their deposition from ca. 9700 to 7500 yr B.P. Talle 1. A piece of oak tump, located in situ approximately 17 in west the profile dated ca. 9900 yr B.P. Thirty-five plant taxa were identified (Table 2). Prickly pear and Gambel oak were the most abundant species in the oldest layer; blackbrush and Mormon tea were common. More species of grass (four) were identified from this sample than from any other. Indian ricegrass was common.

The remaining samples reveal no discernible change until all plant species disappeared from the alcove sometime after 7500 yr B.P. Gambel oak was the most abundant fossil species. Prickly pear was common in an undated sample from the bottom of the profile (GG4) and in the youngest sample (GG1). Other species present in small numbers include box-elder, hackberry, fishhook cactus (*Sclerocactus* sp.), Solomon's seal (*Smilacina* sp.), and Indian ricegrass. Indian ricegrass was the only species present in all samples.

BF ALCOVE.—The four samples from this alcove showed little variation except for a decrease in overall macrofossil abundance as the sterile horizon was approached. The lack of discernible stratigraphy in the test pit and low weights of any one fossil species resulted in the decision to pool the Douglas fir needles from all samples for radiocarbon dating. The two dates merge around ca. 12,000 yr. B.P. (Table 1).

Thirty-nine taxa were identified (Table 2). Most abundant were Douglas fir, bigtooth maple (*Acer grandidentatum*), box-elder, prickly pear, mountain mahogany (*Cercocarpus ledifolius*), and indigobush. Other common species included Gambel oak, currant (*Ribes cf. cercum*), skunkbush, hackberry, and single-leaf ash. Spruce and fir were present, represented respectively by one needle and one cone scale.

HOOPER'S HOLLOW—The oak layer at Hooper's Hollow begins 190 cm from the datum, is up to 100 cm thick, and has been burned extensively. Two samples record plant communities of ca. 10,600 and 12,000 vr B.P. (Table 1).

Only 13 taxa were identified from this alcove, the low number reflecting the lack of preservation because of burning (Table 2). Gambel oak was very common in the Late Pleistocene sample. Uncommon or rare species identified from this sample were prickly pear, rose, box-elder, water birch (*Betula occidentalis*), spruce, and Indian ricegrass.

The Early Holocene sample records chauges in the vegetation during the Pleistocene–Holocene transition. Rose, water birch, box-elder, spruce, and mountain mahogany were no longer at the site. Gambel oak and prickly pear were common. Uncommon or rare species included poison ivy, Solomon's seal, skunkbush, and Indian ricegrass.

Willow Gulch

SHRUB-OX ALCOVE.—The oak layer in Shrub-Ox Alcove began 120 cm from the datum and was about 350 cm thick. Gambel oak was dated from four samples. The oldest date $(23,100 \pm 660 \text{ yr B.P.})$ was on what appeared to be oak wood from a highly degraded part of the macrofossil layer. Only three taxa (oak, hackberry, and mountain mahogany) were recovered from this sample, but the community appears to have been similar to those of the latest Pleistocene in this and other alcoves. The remaining samples record the communities from the Late Pleistocene and the Early Holocene, ca. 12,700 to 8500 yr B.P. (Table 1).

Thirty-eight plant taxa were identified (Table 2). Gambel oak was abundant or very common in all samples. Box-elder and bigtooth maple decreased in abundance from the oldest to the youngest sample. Hackberry was common in the sample dated \$530 yr B.P. but became uncommon by \$520 yr B.P. Prickly pear was never abundant as in the other alcoves, but was only rare or uncommon in the youngest samples. An increased number of grass taxa (five) was observed in the youngest sample. Mountain mahogany was rare or uncommon in all samples. Sagebrush and saltbush were rare or uncommon in the youngest samples as were serviceberry, rose, and brickellbush.

Several species were recorded only from this alcove—willow in the Late Pleistocene sample, and Utah fendlerella (*Fendlerella utahensis*), two sedges (*Carex bella* and *Cladium californicum*), and cottonwood in the youngest sample; all were rare.

OAK HWEN.—Oak Haven has both an oak layer and a rose layer. The stratum containing the rose layer was chosen for profiling. The deposit began 20 cm from the datum and was about 155 cm thick. The oak layer is located to the north of the profile in a pile of wall fall overlain by colian sand.

Three samples were submitted for radiocarbon dating (Table 1). The Gambel oak sample from the oak layer dated ca. 9200 yr B.P. The two lower radiocarbon dates from the profile are reversed relative to the stratigraphy. Rose from the top of the unit dates ca. 11,700 yr B.P., while a sample of spruce twigs combined with ungulate dung from below the rose layer dates ca. 9500 yr B.P. We feel that the spruce date (Beta-25657) is equivocal, as it is a combination of two entirely different species and should not be assigned to spruce or the stratigraphic position until confirmation.

Forty taxa were identified from all samples (Table 2). The youngest sample contained abundant fossils of Gambel oak. Water birch and bigtooth maple were common. Rose is the most abundant species from the dated rose layer. Common species from the layer include Gambel oak, bigtooth maple, and Douglas fir. Rare or uncommon species include sagebrush, boxelder, water birch, prickly pear, and spruce. The two lower, undated layers contain abundant rose and spruce; water birch and box-elder were common.

The Forty-Mile Canyon–Willow Gulch Sequence

The fossil abundances of selected species from both canvons were grouped into a seriated

GG0 GG1 GG2 GG5 GG4 BF HIHI HH2 SOAT SOA2 SOA3 SOA4 OH1 OH2 OH3 OH4 Graze In the Second Lignus sponchides Agrophyron l Oryzopsis hymenoides Stipa Iridens pulchellus (Erioneuron) Browse Abies sp Acer grandidentatum З Acci negundo]] Amaranthus sp. Ambrosia sp. ł Artemisia el dracunenhis ł Atriplex canescens Mriplex el confertifolia] Buccharis sp. <u>.</u>)] -2 ł

r te stoccne and Holocene deposits in BF Alcove, Grobot Grotto, Hooper's Hollow, G. L. S. O. Alco. autheastern Utah.

TABLE 2. Continued.

	GGO	GGI	GG2	GG3	GG1	BF	ШП	11112	5011	50 \2	5033	SOM	ош	0112	OHS	0114
Gutierrezia sp.	_														1	
Haplopappus heterpogon						T									-	
Haplopappus ef. drummondii											1					
Haplopappus sp.				1		-2			1				.2	1	1	
Heterotheca sp.															1	
Hymenoxys sp.						1										
Juniperus scopulorum							1									
Juniperus sp.		Ι														
Lycium pallidum	I															
Mentzelia sp.					1											
Opuntia sp.	3		3		3	-4	3	2	2	I				1	1	-2
Phlox sp.						2		_							2	
Picea sp.						1		1						1	5	3
Polygonum sp.						Ι										
Populus ef. fremontii									1							
Pseudotsuga menziesii						5								3	1	1
Purshia tridentata						Ι									-2	2
Quercus gambelii	1	.3	5	5	3	3	3	1	-5	-4	.5		.)	3	2	1
<i>Quereus</i> sp.	_											1	_			
Rhus aromatica yar. trilobata	1			[1	3	1	1	1	1		_	2		3	3
Ribes ef. cereum						2	_						_			
Rosa woodsii	-		-	_		I	_	.)	2	Ι			1	5	5	5
Salix sp.							_				1					
Sclerocactus sp.	-			-2		_			-							
Shepherdia rotundifolia]]	_										
Smilacina sp.		.2	-2	1		2	-2				_				1	
Sphaeralcea sp.			_]	1						
Toxicodendron rydbergii	1						2		_							
Trifolium sp.	I															
Wyethia sp.	1					I	-									

chronosequence (Fig. 3). Some of the variability seen in the sequence is probably an artifact of sampling and site-to-site differences rather than a real change in vegetation; however, the general trend toward decreasing abundance of mesophytic species is obvious. Douglas fir, spruce, currant, and fir do not appear in the fossil record after 11.690 vr B.P. Willow is also absent from the record after 11.690 vr B.P., but it is common in areas with permanent water in the canvons today. Rose, bigtooth maple, single-leaf ash, and mountain mahogany persist until \$520 yr B.P., while box-elder persists until 7510 vr B.P. These species were not as abundant in samples from after 11,000 yr B.P. as they were in samples prior to that time. Hackberry and water birch become more abundant in the samples after 11,000 yr B.P. Hackberry, box-elder, and single-leaf ash are found restricted to the more mesic habitats in the canyons today. Oak shows little variability in abundance throughout the sequence. The lack of deposits of any kind dating after 7510 yr B.P. suggests that the disappearance of oak from the alcoves by that time was a real event, although the species persist in other cases nearby today.

The more xerophytic species in the sequence are prickly pear, sagebrush, saltbush, skunkbush, blackbrush, and Indian ricegrass. Skuukbush persists in the record until 9150 vr B.P. and was most abundant in samples that date prior to 12,000 yr B.P. It is common and abundant in the canyons today. Prickly pear was most abundant in the sample from ca. 12,100 vr B.P. and is very common in the canyons today. Indian ricegrass, sagebrush, saltbush, and blackbrush show little variability in abundance throughout the time spanned by the record although they are not found in every sample. Today, Indian ricegrass is the most widespread species in the canyons, while the others are frequently encountered in drier habitats.

DISCUSSION

Plant communities that can be described from fossils recovered from the alcoves are much like those found in the canvons today.

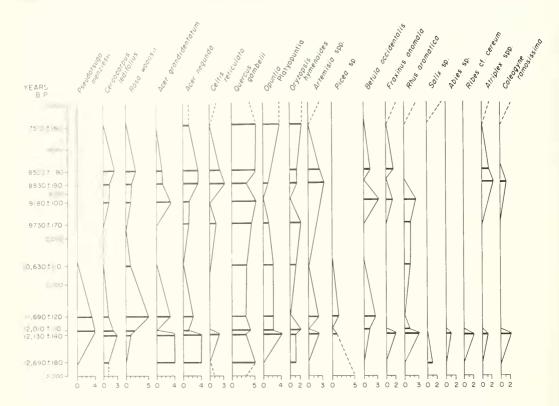


Fig 3. Fossil abundances (rating 0 to 5) of selected plant species from all sites. See text for discussion. Dotted lines refer to inferred previous or known presence today of some species.

Major differences lie in the abundance of mesophytic, relictual species and elevationally depressed, extralocal species dating from the Late Pleistocene and Early Holocene. The most striking similarity is the abundance of Gambel oak in the fossil record and its abundance in some areas of the canyons today. While more verophytic species such as Indian ricegrass and prickly pear have shown changes in abundance, then distributions appear to have changed little in the last 13,000 years.

Inferences regarding changing precipitation regimes based on paleovegetational changes seen in the fossil record are complicated by the listinet possibility that the communities were much nearer the stream in the past than the fossil leposits are today. Three facts suggest that this was true 1. Bison *Bison*, camel cf. *Camelog* and minimoth frequented alcoves in the system as recently is ca. 12,000 yr B.P. Mead and Ageobroid (959, 1992). It seems highly minimate the true area minimal would be able to game on the door estif the stream were located in its present position since at best a steep embankment must be climbed and at worst 10 m of vertical sandstone must be scaled. (2) The existence of Oak Haven. This "active" alcove is wet and is the only alcove currently supporting Gambel oak. We believe that conditions at Oak Haven are analogous to conditions in other alcoves during the Late Pleistocene. (3) All fossil deposits are located behind the dripline, away from direct effects of precipitation, in dry section of the alcoves. This suggests that precipitation was never directly responsible for maintenance of plant communities within the alcoves but that plants were dependent on availability of groundwater flowing from seeps, springs, and the intermittent canyon stream.

Gambel oak is a definitive indicator of climate because it is sensitive to narrow limits of moisture and temperature (Grover et al. 1970, Neilson and Wullstein 1983). Its presence throughout the time spanned by this assemblage makes it suitable for making analogies, at least for temperature. It is found only in areas with

100

mean annual temperatures of 7–10°C (Harper et al. 1985). It is indicative of at least 450 mm of annual rainfall and no less than 250 mm of winter precipitation, but its proximity to a source of groundwater such as a stream modifies these requirements (Grover et al. 1970). The extralocal species will also be used as important indicators of changing temperature and moisture regimes.

Based on the plant taxa identified from the samples (Table 2), we have designated three stages: Late Pleistocene, which includes samples dating >11,000 yr B.P. (including OH3); Early Holocene, between 11,000 and 8000 yr B.P.; and Terminal Early Holocene, between 8000 and 7000 yr B.P.

Chronology of Paleoenvironmental Change

LATE PLEISTOCENE ENVIRONMENT (>11,000 YR B.P.).—Elevationally depressed, montane species are the hallmark of Late Pleistocene plant communities. In Forty-Mile Canyon and Willow Gulch, spruce occurred as much as 900 m lower than today while water birch was up to 80 m lower. Douglas fir, currant, and mountain mahogany exhibited depressions between 260 and 300 m, and bigtooth maple was as much as 140 m lower. All these species (with the possible exception of bigtooth maple) are extralocal and probably occur no closer than the Aquarius Plateau, about 70 km to the north.

Relictual, mesophytic species were abundant during this time. Species that appear to have been common in the Late Pleistocene. such as rose and box-elder are rare or uncommon in the canyons today. Where they do occur, they are restricted to streamside or other shady, wet situations where seasonal droughts do not occur. While Gambel oak is common is some areas of the canyons, it is also restricted to more mesic habitats. The only important xerophytic plant in the assemblages is prickly pear. The plant community of the earlier time can be interpreted as representing a somewhat cooler environment with more available moisture than is found in the alcoves today. Whether these were just seasonal differences cannot be stated at this time.

The Escalante River served as a route by which high-elevation species such as Douglas fir and spruce were able to disperse into the lower canyons. Mean annual temperature in the Aquarius Platean today is about 2°C. However, prickly pear, which is common in the fossil sam-

ples, is rarely found in areas with mean annual temperatures below 6°C (Betancourt 1984) Gambel oak, also very common or abundant in the fossil assemblages, is found only in areas with mean annual temperatures of 7-10°C (Harper et al. 1985). Mean annual temperature in the Escalante Basin today is 10–12°C (Webb 1985). It is unlikely that cooling in the Escalante Basin during the Late Pleistocene exceeded the 3-4°C postulated by Betancourt (1984) for higher-elevation sites in the Paradox Basin. We interpret that mean annual temperature extremes in the Escalante River area may have been little different from those of today. Cold air drainage from the Aquarius Plateau and increased local water availability may have been responsible for the persistence of montane species in the canyons.

Although temperatures in the Escalante Basin may have been little different from what they are today, it is apparent that the alcoves were much wetter. We hypothesize that this was attributable to increased groundwater rather than increased local rainfall. During the Late Pleistocene these canyons contained much more valley fill than they do today, and stream base level was up to 50 m higher.

Stream entrenchment can take place during moist periods when plant cover is abundant or plentiful in the upper reaches of the stream (Antevs 1955). If rainfall was greater at higher elevations during the Late Pleistocene, as is suggested by most workers (Phillips 1977, 1984, Spaulding and Van Devender 1980, Betancourt 1984, Davis et al. 1984), then Forty-Mile and Willow creeks probably began to become entrenched during the Late Pleistocene. Because of entrenchment, the erosion of valley fill continued and groundwater levels began to decrease.

EARLY HOLOCENE ENVIRONMENT (11,000 TO \$000 YR B.P.).—The major reorganization of the plant communities during this time noted by Betancourt (1954) and other workers on the Colorado Plateau is apparent in this assemblage also. The only extralocal species found in the fossil assemblages were bigtooth maple and mountain mahogany. While still at lower elevations than they are found today, elevational depressions decreased to 30 m and 200 m, respectively. Fossils of these and other relictual, mesophytic species such as rose persisted but were less abundant than in the previous stage. Even Gambel oak decreased slightly in some of it is apple. Here are no apparent increases in the abundance of xerophytic plants, but decreasing abundances of mesophytic plants are endence of changes in both temperature and moisture regimes.

Data for Forty-Mile Canyon and Willow Gulch appear to indicate two shifts in the flora that are similar to those seen in the Paradox Basin, Extralocal species except rose drop from the record prior to ca. 10,600 yr B.P. Bigtooth maple rose, and momitain mahogany recover for a short time between ca. 10,000 and \$500 yr B P before dropping from the record. Gambel oak increased in abundance and hackberry became common during this time, indicating that summer moisture may have become more reliable with the establishment of the monsoonal boundary.

Shifts in the floras seen in the Escalante Basin during the Early Holocene indicate that prior to 10,600 vr B.P. temperatures or temperathre extremes began to increase and moisture availability was less reliable. This resulted in decreased abundances of mesoplivtic plants and the upslope retreat of Douglas fir and spruce. After 10.600 vr B.P., the recovery of mesophytic species such as bigtooth maple indicated that moisture availability became more reliable again although most species do not appear to have been as abundant as in the latest Pleistocene. This moisture is still more attributable to increased groundwater due to higher stream base level. Groundwater levels and rate of stream entrenchment fluctuated during this stage in response to fluctuating rainfall amounts as the summer monsoon moved to its present

Mast date of ca. \$700 yr B.P. on Gambel oak leaves at Cowboy Clave is interpreted as marking the inception of a more veric elimate. Spaulding and Van Devender 1980). The sample that dates c1 \$500 yr B.P. from Shrub-Ox Alcove contains "bird int Gir bel oak anthers. Gambel oak on of trease ly peric sites often fails to produce mathe tennic flowers but produces an abundance otomace allar Creeman et al. 1981). We behe will be also also date marks the termination of more components in the alcoves, with the stream that the almomore than 10 m above its present of the alcoves were still wetter than they are not commost of the stage, but continued stream and a source t enhuinated in drier alcove environe of the he end of the Early Holocene. The the progs became

less reliable or completely dried up. Coupled with warmer seasonal temperatures, this drying resulted in the disappearance of most mesophytic species by the end of our stage.

TERMINAL EARLY HOLOCENE ENVIRON-MENT (\$000 TO 7000 YR B.P.).—The one sample from this time period is from Grobot Grotto. The fact that there is only one sample in itself suggests a major change in the environment after ca. \$500 yr B.P. The sample contains only Gambel oak and prickly pear in any quantity. No plant macrofossils are found above this layer in Grobot Grotto, and none above layers dating a thousand years earlier in Shrub-Ox Alcove. This sample appears to mark the beginning of extremely dry environments in the alcoves and the establishment of the present environmental regime.

Because of its ability to reproduce vegetatively (Cottam et al. 1959), Gambel oak is able to persist in areas where seedlings are unable to become established. The stand of oaks that lived in Grobot Grotto until 7510 vr B.P. likelv represents the last hold-outs before the local water table became so low that even they died. The disappearance of Gambel oak and all plants from the alcoves is interpreted as representing warmer, and at least seasonally drier, climates, and therefore the entrenching of the streambed. Stream base level was probably very near its present position by this time, leaving the alcoves high and dry, without groundwater resources to feed the seeps and springs that had previously supported the plant communities.

Biogeographie and Paleoclimatic Considerations

The Escalante River appears to have served as a major migrational route for high-elevation and mesophytic species during the Late Pleistocene. It is likely that stream base level was as much as 50 m higher than at present. At the lower elevational limits of a plant, high temperatures and deficient soil moisture produce transpiration stress in established individuals and reduce the potential for germination and seedling establishment. Relaxation of these controls can be accomplished by lowering summer temperature extremes, which would result in increased effective moisture, or by increasing precipitation (Betancourt 1984). Since drought was not a limiting factor, the elevational depression of montane species observed in this area was probably primarily the result of cooler summer temperatures, possibly facilitated by cold air drainage from the Aquarius Plateau.

Southerly displacement of the polar jet stream during the Late Pleistocene has been proposed, based on paleovegetation (Van Devender and Spaulding 1979) and modern plant distributions (Neilson and Wullstein 1983). In southeastern Utah this would result in milder. wetter winters and cooler drier summers an equable climate (Betancourt 1984). This interpretation corresponds well with the interpretation of the assemblages from our study as well as with those of most other workers (except Cole) on the Colorado Plateau, Gambel oak was at low-elevation sites in these canyons and at Cowboy Cave and Bechan Cave. Today, its northern limit coincides with the polar jet stream at 41° N latitude. The fossil distribution of Gambel oak suggests that the polar jet stream was displaced into the central Plateau at about 38° N latitude during the Late Pleistocene.

The terminal date for woodland communities in the Southwest is consistently younger than the traditional date of ca. 11,000 vr B.P. for the end of the Pleistocene. However, in North America this boundary is generally believed to be time-transgressive (Watson and Wright 1980) and appears to vary with latitude. Transitional communities with mesic characteristics persisted in many areas until the end of the Early Holocene, ca. 7800 yr B.P., when woodland species disappeared from modern desert areas (Van Devender 1977). The changes in vegetation during this time involved a gradual decrease in the abundance and number of woodland species and a relative increase in the importance of desert species, many of which were already present (Phillips 1977). In the eastern Grand Canvon, peak values for vegetation change (species flux) were recorded between 12,000 and 8000 vr B.P. Cole (1985) believes that Wisconsin species tended to disappear prior to the establishment of modern species. The major reorganization of vegetation zones during this time precludes the use of elevational analogs (Betancourt 1984).

In our study we postulate that warmer temperatures and increased drought stress due to fluctuating groundwater levels resulted in the upslope retreat of montane conifers and decreased abundance of mesophytic species during the Early Holocene. Mesophytic species showed a brief recovery late in our stage before disappearing from the alcoves ca. 8500 vr B.P. Sexual reproduction in oaks stopped by the end of the stage, as evidenced by the abundance of male catkins in samples from Shrub-Ox Alcove. The polar jet stream retracted to the north as the summer monsoonal boundary approached its current position. This would result in higher annual temperatures and summer extremes, less available moisture, more reliable summer precipitation, and a prolonged spring drought.

The senescence and death of oak trees and the disappearance of all vegetation from the alcoves in the canyons by ca. 7500 yr B.P. are interpreted as the result of warmer temperatures and the establishment of stream base level near its present position. Most other workers on the Colorado Platean have interpreted their records as reflecting greater effective moisture during this time. However, our record reflects more veric conditions as a result of decreased groundwater and possibly seasonally drier conditions. The disappearance of Gambel oak from low-elevation sites in the central Colorado Plateau may represent a northward retraction and/or upslope retreat of the species as conditions at lower elevations became too hot and dry. Conversely, the xerophytic shrub live oak, whose northern boundary currently coincides with the monsoonal boundary, and Pinus edulis expanded northward in response to hotter, drier conditions, similar to Anteys' Altithermal, Living populations of relict hybrids between the two oak species as well as between P. edulis and P. monophylla occur at the Middle Holocene northern limit of shrub oak and *P. edulis* and the southern limit of Gambel oak and P. monopluglla (Lanner 1974, Neilson and Wullstein 1983). Today shrub live oak and P. edulis reach their northern limits far south of the relict hybrid populations.

Cole (1981) suggests that a northward shift of the summer monsoon and polar jet stream would explain his xerie record for the eastern Grand Canyon, while the same scenario is invoked to explain the occurrence of the hybrids and is consistent with a recent study of modern and fossil distributions of apomictic and sexually reproducing populations of muttongrass (*Poa feudleriana*) on the Colorado Plateau (Soreng and Van Devender 1959). It would also explain the dry record for the Escalante Basin. Those records from the central Plateau that are interpreted as wet are from higher-elevation sites where wetter, cooler situations could have persisted.

SUMMARY.

The record from Forty-Mile Canvon and Willow Gulch reflects at least seasonally and/or locally wetter, more equable climates in the Late Pleistocene. The macrofossils record gradual warning and drying, which became extreme sometime after \$500 yr B.P. so that all vegetation disappeared from the alcoves by 7500 yr B.P. The increased dryness is directly attributable to falling stream base levels and decreased ground-water and only indirectly to changing amounts and/or seasonality of precipitation.

Our record is in general agreement with other Colorado Plateau records except that it appears to reflect at least seasonally drier conditions during the Middle Holocene. This is probably because our sites are at lower elevations than the others. Further studies of similar macrobotanical deposits in the surrounding area, if they exist, are in order. Expansion of this record could delineate the changing position of the northern limit of Gambel oak and, by extension, the geographic positions of both the monsoon and polar jet stream throughout the late Quaternary. Additional data from this area would also help refine the geographic and temporal boundaries of both wet and dry altithermals. Additional paleobotanical studies in the area are necessary if the late Quaternary paleoecology of the central Colorado Platean is to be adequately understood.

ACKNOWLEDGMENTS.

We thank Louella Holter (Bilby Research Center for typing the manuscript. We appreciate the following people for their help in the field Lany Agenbroad, Liz Barnosky, John Ben-Jamin, Brian and Karen Cluer, and Emilee Mead Emilee provided all photography and Ir ilting The Rocky Mountain Region, National Park Service Denver office, and Glen Canyon National Recreation Area provided logistic and uration assistance. We appreciate the special and continued help of Adrienne Anderson and Bob Schuller, National Park Service). Funding for this project was provided by National Science Foundation grants FAR \$705287 and \$\$15217 Mond and L. D. Agenbroad, and National Factor ice contract CS-1200-A-4062 to Agenbroac.

LITERATURE CITED

- ALBEE, B. J. 1979. A guide to the identification of seeds used by prehistoric Indians. Pages 283–321 in J. D. Jennings, ed., Swallow Shelter, University of Utah Anthropology Papers 103.
- ANTEVS. E. 1955. Geologic-climatic dating in the West. American Antiquity 20: 317–335.
- BETANCOURT J. L. 1984. Late Quaternary plant zonation and climate in southeastern Utah. Great Basin Naturalist 44: 1–35.
- ______. 1990. Late Quaternary biogeography of the Colorado Plateau. Pages 259–292 in J. L. Betancourt, T. R. Van Devender, and P. S. Martin, eds., Packrat middens. The last 40,000 years of biotic change. University of Arizona Press, Tucson, 467 pp.
- COLE, K. L. 1951. Late Quaternary environments in the eastern Grand Canyon: vegetational gradients over the last 25,000 years. Unpublished doctoral dissertation, University of Arizona, Tucson. 170 pp.
- _____. 1985. Past rates of change, species richness, and a model of vegetational inertia in the Grand Canyon, Arizona. American Naturalist 125: 289–303.
- COTTAM, W. P., J. M. TUCKER, AND R. DROBNICK 1959. Some clues to Great Basin postpluvial climates provided by oak distributions. Ecology 40: 361–377.
- DWIS, O. K., L. D. AGENBROAD, P. S. MARTIN, AND J. I. MEAD 1984. The Pleistocene dung blanket of Bechan Cave, Utah. Pages 267–282 in H. H. Genoways and M. Dawson, eds., Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday. Special Publications of the Carnegie Museum of Natural History 8.
- DELORIT R. J. 1970. Illustrated taxonomy manual of weed seeds. Agronomy Publication, River Falls, Wisconsin. 175 pp.
- ELMORE, F. H. 1976. Trees and shrubs of the Southwest uplands. Southwest Parks and Monuments Association, Tucson. 214 pp.
- FREEMAN, D. C., E. D. MCARTHUR, K. T. HARPER, AND C. BLAUER 1981. The influence of environment on the floral sex ratio of monoecious plants. Evolution 35: 194–197.
- GOULD, F.W. 1951. Grasses of southwestern United States. Univsity of Arizona Press, Tucson, 352 pp.
- GROVER, B. L., E. A. RICHARDSON, AND A. R. SOUTHARD 1970. Quercus gambelii as an indicator of climatic means. Proceedings of the Utah Academy of Science 47: 187–191.
- HANSEN, R. 1980. Late Pleistocene plant fragments in the dung of herbivores at Cowboy Cave. Pages 179–189 in J. D. Jennings, ed., Cowboy Cave. University of Utah Anthropology Papers 104.
- HARPER, K. T., F. J. WAGSTAFF AND L. M. KUNZLER 1985. Biology and management of the Gambel oak vegetative type: a literature review. USDA INT-179, Intermountain Forest and Range Experiment Station, Ogden, Utah.
- LANNER, R. M. 1974. Natural hybridization between *Pinus edulis* and *Pinus monophylla* in the American Southwest. Silvae Genetica 23: 108–116.
- MARTIN A. C., AND W. D. BARKLEY 1961. Seed identification manual. University of California Press, Berkeley.
- MEAD J. L. WND L. D. AGENBROAD 1989. Pleistocene dung and the extinct herbivores of the Colorado Plateau, Southwestern USA, Cranium 6: 29–44.

___, 1992. Isotope dating of Pleistocene dung deposits from the Colorado Plateau, Arizona and Utah. Radiocarbon 34: 1–19.

- MEAD, J. L. D. AGENBROAD, O. K. DAVIS, AND P. S. MARTIN 1986, Dung of *Mammuthus* in the arid Southwest, North America, Quaternary Research 25: 121– 127.
- MORRIS, M. S., J. E. SCHMAUTZ, AND P. F. STICKNEY 1962, Winter field key to the native shrubs of Montana. Montana Forest and Conservation Experiment Station, Montana State University and Intermonntain Forest and Range Experiment Station, USFS, USDA.
- NEILSON, R. P., AND L. H. WULLSTEIN, 1983. Biogeography of two sonthwest American oaks in relation to atmospheric dynamics. Journal of Biogeography 10: 275–297.
- PHILLIPS, A. M. HI, 1977, Packrats, plants and the Pleistocene in the lower Grand Canyon. Unpublished doctoral dissertation, University of Arizona, Tucson, 123 pp.
 - 1984. Shasta ground sloth extinction: fossil packrat midden evidence from the western Grand Canyon. Pages 148–158 in P. S. Martin and R. G. Klein, eds., Quaternary extinctions: a prehistoric revolution. University of Arizona Press, Tucson, 892 pp.
- SORENG, R. J., AND T. R. VAN DEVENDER 1989. Late Quaternary fossils of *Poa fendleriana* (muttongrass): Holocene expansions of apomicts, Southwestern Naturalist 34: 35–45.
- SPAULDING, W. G., AND K. L. PETERSEN 1980. Late Pleistocene and early Holocene paleoecology of Cowboy Cave. Pages 163–177 in J. D. Jennings, ed., Cowboy Cave, University of Utali Anthropology Papers 104.
- SPAULDING, W. G., AND T. R. VAN DEVENDER 1980. Late Pleistocene montane conifers in southeastern Utah.

Pages 159–162 in J. D. Jennings, ed., Cowboy Cave, University of Utah Anthropology Papers 104.

- TANNER, V. M. 1940. A biotic study of the Kaiparowits region of Utah. Great Basin Naturalist 1: 97–126.
- VAN DEVENDER T. R. 1973. Late Pleistocene plants and animals of the Sonoran Desert: a survey of ancient packrat middens in southwestern Arizona. Unpublished doctoral dissertation. University of Arizona, Tucson. 179 pp.
 - _____. 1977. Holocene woodlands in the southwestern deserts. Science 195: 159–192.
- VAN DEVENDER T. R., AND W. G. SPAULDING 1979. Development of vegetation and elimate in the southwestern United States. Science 204: 701–710.
- WATSON, R. A., AND H. E. WRIGHT, JR. 1980. The end of the Pleistocene: a general critique of chronostratigraphic classification. Boreas 9: 153–163.
- WEBB, Ř. H. 1985. Late Holocene flooding on the Escalante River, south-central Utah. Unpublished doctoral dissertation, University of Arizona, Tucson. 204 pp.
- WELSH, S. L. 1986. *Quercus* (Fagaceae) in the Utah flora. Great Basin Naturalisi 46: 107–111.
- WELSH, S. L., N. D. ATWOOD AND J. R. MURDOCK 1978, Kaiparowits flora. Great Basin Naturalist 35: 125–179.
- WELSH, S. L., N. D. ATWOOD, S. GOODRICH, AND L. C. HIGGINS 1987. A Utah flora. Great Basin Naturalist Memoir 9. Brigham Young University, Provo, Utah. 894 pp.
- WITHERS, K. 1959. Late Quaternary vegetation and climate of Forty-Mile Canyon and Willow Gulch, in the central Colorado Plateau. Unpublished master's thesis, Northern Arizona University, Flagstaff, 71 pp.

Received 2 December 1991 Accepted 7 December 1992